ORIGINAL ARTICLE

Acclimatization of European beech (*Fagus sylvatica* L.) leaves first year after planting into different light conditions of young spruce stand

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ABSTRACT

The study presents the results of investigation on reaction of beech (*Fagus sylvatica* L.) leaves observed next year after planting seedlings in different positions in a young spruce stand located in upper mountain conditions. The methods of chemical analyses and assessments of chlorophyll fluorescence were applied with the aim to evaluate a course of leaf adaptation. In the young spruce stand located in the Karkonoše Mts, bare root beech seedlings after cultivation in full light were planted into three main positions to spruce trees (under the crown, within crown perimeter and in stand gaps). Next year after planting, the total biomass, leaf nutrient content and chlorophyll fluorescence parameters were evaluated. The beech trees planted under spruce (*Picea* sp.) crowns had significantly lower specific leaf mass and the mean leaf area was decreasing from shade to sun. Differences in nutrient contents were not significant between the treatments. We found significantly higher values of minimal (F_0) and the maximum fluorescence (F_m) as well as of the maximum quantum yield of PSII photochemistry (F_v/F_m) in the leaves of beeches growing under the spruce crown. Significant differences among treatments were found also in the courses of the values of maximum fluorescence yield Y(II) and nonphotochemical quenching (NPQ). Our study indicated that bud forming processes are only partially responsible for physiological properties of beech leaves evaluated next year after planting. Photosynthetic performance is also influenced by actual growing conditions. A great part of acclimation occurs already in the first year after planting (change of the light conditions). We speculate that this phase of gradual acclimation of the assimilation apparatus can be one of the reasons of physiological weakening of the plant after planting to different light environment.

INTRODUCTION

Seedlings of particular tree species in forest nurseries are usually cultivated in uniform light conditions: in full light or partial shade. The conditions of cultivation influence the assimilation apparatus and formation of new buds. Growing environment of seedlings completely changes after planting. First of all, during underplanting and early starting gradual reconstructions of young coniferous substitute tree species interplant-

ings[1] (Balcar and Kacálek 2008), seedlings can experience considerable changes and variability of light environment. Common reaction of plants to planting is an overall response called tree transplanting shock. The question remains: how is tree transplanting shock related to a rate of plant leaf adaptation to new light conditions of a given forest site after planting?

Quantity and quality of the assimilatory apparatus have an important role for tree growth and its production ability. Leaf chemical analysis offers information on supply of nutrient elements to trees (Kopinga and van den Burg 1995). In accordance with the study of Meier *et al.* (2005), the nutrient content in leaves is only partly dependent on parent stock material. There were found relations of different light environments to the nutrient content in beech leaves (Johnson *et al.* 1997; Kazda *et al.* 2004; Špulák 2008).

Chlorophyll *a* fluorescence is a non-destructive method of monitoring photosynthesis, based on the principal work of Kautsky and Hirsch (1931). A basis for the application of this method is the relation of chlorophyll fluorescence to the capacity of photosynthesis (Roháček 2002). Being measured and analyzed adequately, chlorophyll fluorescence makes it possible to provide detailed information on what is going on inside the photosynthesizing organism (Schreiber 2004). This method is commonly applied to many fields of forest ecology (Ball *et al.* 1994; Mohammed *et al.* 1995, 2003).

Plants, when exposed to high or low irradiance during growth, react with a variety of adaptation mechanisms, i.e. formation of sun and shade leaves as well as sun and shade chloroplasts (Lichtenthaler 1981). Plants are also exposed to a variety of biotic and abiotic stressors that affect their growth, physiological functions and yield. Stressors affect either directly or indirectly photosynthetic apparatus functions as well as performance of leaves and often modify their optical and fluorescence properties (Lichtenthaler *et al.* 2000).

The European beech (*Fagus sylvatica* L.) is a shade tolerant tree species. Shade tolerance is especially important during juvenile stages of natural regeneration, because juveniles in the understorey are likely to be

subject to shade suppression (Madsen 1995). The beech is the most common broadleaved tree species introduced into coniferous monocultures in mountain locations in the Czech Republic in the frame of activities towards stand reconstruction and stabilization (Balcar and Kacálek 2008; Hobza *et al.* 2008).

Limited information is available to accurately predict beech seedling physiological responses to suddenly changed environment due to replanting. Studies available are done mostly with potted seedlings under highly controlled conditions (Cochard *et al.* 1999; Johnson *et al.* 1997; Welander and Ottosson 1998; Tognetti *et al.* 1997) or within natural regeneration sites established in shade (Reynolds and Frochot 2003). Johnson *et al.* (1997) described fairy large acclimation potential of beech trees in natural sites, determined by both physiological and biochemical flexibility. According to Küppers and Schneider (1993), beech seedlings grown in shade are well adapted to dynamic light environments. In the study of Tognetti *et al.* (1997), one-year-old seedlings transferred from low to high light conditions during the vegetation period, in the 20-day measurement period never fully acclimated to photosynthesis levels of seedlings growing continuously in high light environment. Epron *et al.* (1995) in the study on beech primary and secondary growth flushes found that the leaves of the second growth flush were better adapted to high light conditions. These authors stated that beech ability to produce 2 types of leaves mostly on nutrient rich soils might allow rapid adaptation to changes in microclimate during regeneration. Johnson *et al.* (1997) observed that one-year-old beech seedlings grown in pots in three different light environments, i.e. understorey of mature beech forest, gaps and clearings within mature beech forests, exhibited differing diurnal gas exchange patterns.

The aim of this study was to compare selected parameters of the assimilatory apparatus of the European beech one year after planting into different positions in a young spruce stand situated in upper mountains with the use of leaf chemical analysis and chlorophyll *a* fluorescence. We hypothesized, that already first year after planting: 1) different light conditions of planting positions, i.e. under spruce crown, on the crown perimeter and in stand gaps would alter leaf properties, 2) the concentration of nutrients in beech leaves planted in shade of spruce crowns would differ from those planted in sunny

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[1] Interplanting – planting young trees among existing natural regeneration or previously planted trees of similar age (Natural Resources Canada. 1995. Silvicultural Terms in Canada. 2nd ed. Natural Resources Canada, Canadian Forest Service, Ottawa, ON, 109 p.).

locations in stand gaps and 3) seedlings planted in the gaps would have greater efficiency of photochemical processes compared to those planted under spruce crowns.

MATERIAL AND METHODS

Experimental plantation

F. sylvatica bareroot seedlings, which originated from mountain locations of the natural forest area 21 (Jizerské hory Mts. and Ještěd Mnt.), were cultivated in full light in the forest nursery located 500 m above sea level. In autumn 2007, after one year of intensive cultivation (mean seedling height was 30 cm) the seedlings were interplanted to the young spruce forest stand located in upper mountains, within the Lesní bouda research plot in the Krkonoše Mts. (1,080 m a.s.l., acid spruce forest site type, ridge location). The spruce stand was about 20-year-old mixture of the Norway spruce [*Picea abies* (L.) Karsten, autochthonous] and the blue spruce (*Picea pungens* Engelm. – substitute tree species introduced in the period of air pollution disaster) with mean height of 2.4 m and mean density of 2,400 trees per hectare. Mean height of spruce lowest branches was 40 cm. Beech seedlings were planted into three positions to spruce trees: under the crown, within the crown perimeter and in gaps between spruce trees.

Leaf area and leaf chemical analysis

In August 2008, next year after planting, the total biomass of leaves of 11 randomly selected beeches in each stand position (crown, perimeter and gap) was taken for chemical analyses. Prior to the analyses, the number of leaves was assessed and leaf area of 10 randomly selected leaves of every sample was measured using a scanner and ImageJ 1.40 software.

Afterwards all samples were air-dried, followed by drying at 70°C in the laboratory and then weighted. The nutrient content was evaluated after mineralization with the use of mineral acid. Because of low amounts of leaf dry matter obtained, leaf material from 2–4 plants was merged and 4 mixed samples for each stand position were analyzed. Total nitrogen (N) concentration was analyzed by the Kjeldahl procedure and phosphorus (P) concentration was determined colorimetrically. Atomic Adsorption Spectrophotometry was used to determine total potassium (K) concentration by flame emission, while

calcium (Ca) and magnesium (Mg) were determined by atomic adsorption after addition of lanthanum.

Measurements of chlorophyll *a* fluorescence

The samples of leaves from randomly selected beeches which were planted in the three different positions were taken for analyses of chlorophyll *a* fluorescence. Before measurements, sample small branches were dark-adapted for at least 30 minutes at ambient temperature. Central parts of leaves of 4 randomly selected samples were prepared for one measurement. In total, 5 leaves of 6 plants from each position were analyzed by Imaging-PAM Chlorophyll Fluorometer (Heinz Walz GmbH) controlled by PC software ImagingWin V2.32. At each leaf sample one area of interest with the size approximately 0.25 cm^2 was defined to obtain average parameters of chlorophyll *a* fluorescence. Intensity of pulse-amplitude-modulated measuring light was set to 3 mmol m^{-2} s^{-1}, pulse frequency 1. First, there was perfomed measurement of "dark fluorescence parameters" (minimal fluorescence – F_0, maximal fluorescence – F_m) using saturation pulse of width 800 ms and intensity of photosynthetically active radiation (PAR) 2400 μmol quanta m^{-2} s^{-1}, and then absorptivity (Abs.) was measured with the use of Fluorometer. The absorptivity image is a measure of a fraction of the incident Red-light which is absorbed by a leaf sample (Walz 2004). This was calculated by software from the R- and NIR-images using the formula:

$$\text{Abs.} = 1 - \text{R/NIR.}$$

Maximum quantum yield of PSII photochemistry (F_v/F_m) was calculated by software according to the formula

$$F_v/F_m = \frac{F_m - F_0}{F_m}.$$

The standard dark-light induction curve in 20 second steps (18 steps, actinic light intensity 8 mmol.m^{-2}.s^{-1} PAR) was ensued and quenching coefficients were calculated. To provide information about dark-light induction, maximum fluorescence yield in the light-adapted state of leaves (Fm') was selected.

Subsequently, the rapid light curve (RLC) in 22 steps of 10 sec interval (intensities up to 1,414 mmol.m^{-2}.s^{-1} PAR) was measured. For the purpose of this study the presented parameters of RLC are effective PS II quantum yield [Y(II)] computed according to the formula

$$Y(II) = \frac{(F_m' - F)}{F_m'},$$

non-photochemical quenching (*NPQ*) as

$$NPQ = \frac{(F_m - F_m')}{F_m'},$$

and electron transport rate (ETR) as

$$ETR = Y(II) \times PAR \times 0.5 \times Abs.$$

For more details on the Imaging PAM instrument, measuring and parameters measured see Walz (2003).

Statistical analyses

The differences in analyzed parameters were checked for significance using analysis of variance (ANOVA) and Tukey's HSD Post Hoc Test. Firstly, homogeneity of variances and normality of distributions were tested, and to improve normality the Box-Cox transformation was applied.

Shapes of Fm', Y(II), NPQ and ETR curves were tested to verify differences among beech positions in the stand (treatments) by comparing confidence intervals, computed using the formula:

$$\bar{x} \pm 1.96 \left(\frac{\sigma}{\sqrt{n}} \right),$$

where σ = standard deviation and n = number.

Computations were carried out with the use of Unistat 5.601 software at the probability level 0.05.

Results

One year after planting into the young spruce stand beech sample trees had from 7 to 38 leaves (average 17.6). Due to the transplanting shock many beeches had a drying terminal shoot, and height increment was very rare. Average leaf area decreased with lowering potential share of spruce individuals: the beeches planted under spruce crowns had the highest average leaf area, and the beeches in stand gaps had the lowest average leaf area, yet these differences were not significant (Tab. 1). There were found not significant differences between mean weights of leaf dry matter, but specific leaf mass of the leaves of beeches planted under the spruce crown was significantly lower when compared with other treatments (0.38 g.dm^{-2} compared to 0.49 g.dm^{-2} in perimeter treatment and 0.50 g.dm^{-2} in gap treatment).

Tab. 1. Mean leaf area, mean weight of leaf dry matter and mean specific leaf mass of beeches planted in three different positions. Different letters between treatments indicate statistical differences (ANOVA, Tukey's HSD Post Hoc Test)

Treatment	Leaf area		Dry matter of leaf		Specific leaf mass	
	cm^2	S.D.	g	S.D.	g.dm^{-2}	S.D.
Crown	5.017	1.123	0.0184	0.0039	0.376**b**	0.0769
Perimeter	4.840	1.460	0.0239	0.0080	0.493**a**	0.0916
Gap	4.253	1.125	0.0217	0.0076	0.502**a**	0,0627

Note: Crown – beeches planted under the crown of young spruce, perimeter – planted within the perimeter of the spruce crown, gap – planted in the gap between spruce trees. Conf. – confidence value.

No significant differences were found among mean concentrations of analyzed macronutrients in the leaves of beeches growing in one of the three positions (Tab. 2). Mean values of concentrations of N, P and K lowered in the direction from crown to gap position, while Ca and Mg concentrations indicated a reverse trend.

Tab. 2. Mean contents (%) and standard deviation (S.D.) of nutrients in leaves of beeches according to different position in spruce stand one year after planting in the Lesní bouda research plot (n = 4 per treatment). No statistical differences (ANOVA)

Treatment	N		P		K		Ca		Mg	
	mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.
Crown	2.24	0.179	0.408	0.060	0.55	0.101	0.26	0.047	0.236	0.028
Perimeter	1.97	0.193	0.366	0.098	0.44	0.018	0.40	0.057	0.253	0.030
Gap	1.96	0.138	0.349	0.050	0.42	0.045	0.40	0.106	0.285	0.033

Treatment explanations in Tab. 1.

From the analyses of chlorophyll *a* fluorescence, we found a decrease of mean dark fluorescence parameters in the leaves of beeches from shady to sunny conditions. The beeches planted under the spruce crown had significantly higher minimal (F_0), maximal fluorescence (F_m) as well as maximal quantum yield of PSII photochemistry compared to the beeches in stand gaps (F_v/F_m 0.852 vs. 0.828). No significant differences were observed in absorptivity, however mean values indicated lowering of this parameter from the sun to the shade.

Plants grown in the analyzed three positions in the spruce stand showed a completely different response to application of saturation pulses during the measurements of dark-light induction curves. We found significantly lower values (run) of the maximum fluorescence yield in the light-adapted state of leaves (Fm') with growing potential irradiance of location – from the shade position – under crown position to the sunny position in gap (Fig. 1).
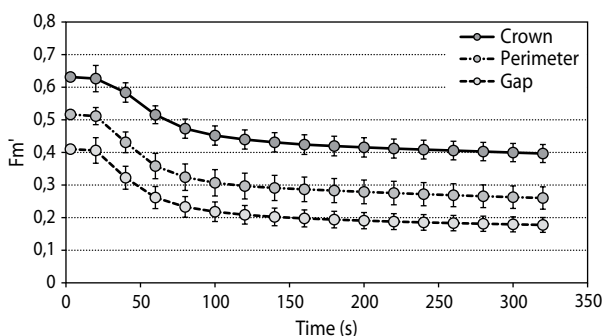
Fig. 1. Maximum fluorescence yield in the light-adapted state of leaves (Fm') with confidence intervals of beeches leaves according to different positions in spruce stand. Treatment explanations in Tab. 1

Results of the light response curve analyses are demonstrated using light response curves of effective PS II quantum yield – Y(II), nonphotochemical quenching – NPQ and Electron Transport Rate – ETR (Fig. 2). In the course of Y(II), we observed the quickest decrease of the response curve of the beeches planted under the spruce crown, and the slowest was observed in the beeches planted in gaps, but these differences were inconsiderable and not statistically significant. In contrast, significant differences were found between NPQ curves of the beeches planted under spruce crowns and in stand gaps. The plants from gaps showed also higher

run of the nonphotochemical quenching than the beeches from the crown perimeter, nevertheless, the curves did not differ statistically (Fig. 2).
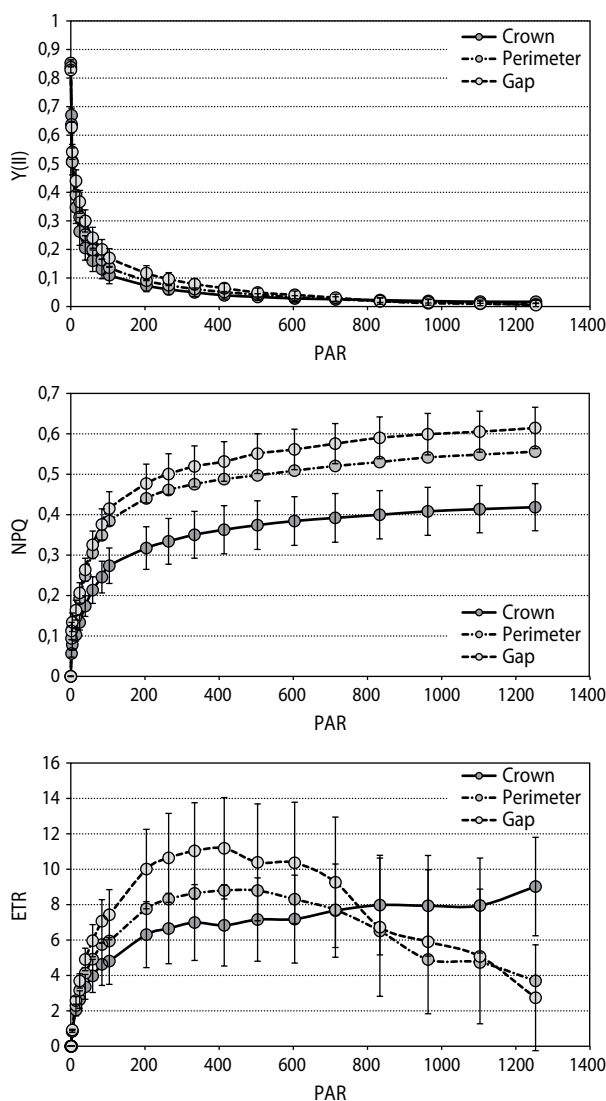
Fig. 2. Light response curves of effective PS II quantum yield – Y(II), nonphotochemical quenching – NPQ and Electron Transport Rate – ETR [$mmol.m^{-2}.s^{-1}$] of beeches according to different position in spruce stand one year after planting in the Lesní bouda research plot. PAR – photosynthetically active radiation ($mmol.m^{-2}.s^{-1}$), error lines show confidence intervals (P = 0.05). Treatment explanations in Tab. 1

Parameter ETR showed a completely different curve shapes for shaded and illuminated trees. The gap and perimeter beeches reached maximum values of ETR in light intensity of about 400 to 500 $mmol.m^{-2}.s^{-1}$ PAR, in

Tab. 3. Minimal (F0), maximal (Fm) fluorescence, maximal yield of PSII photochemistry (Fv/Fm) and absorptivity (Abs.) of beeches leaves according to different position in spruce stand one year after planting in the Lesní bouda research plot (n = 6 per treatment, 5 times repeated). Different letters between treatments indicate statistical differences (ANOVA, Tukey's HSD Post Hoc Test)

Treatment	F0		Fm		Fv/Fm		Abs.	
	mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.
Crown	0.091 a	0.0107	0.631 a	0.1134	0.853 a	0.0299	0.773	0.0164
Perimeter	0.083 a	0.0131	0.516 b	0.0739	0.838 ab	0.0252	0.774	0.0235
Gap	0.068 b	0.0132	0.410 c	0.1118	0.828 b	0.0297	0.782	0.0196

Treatment explanations in Tab. 1

higher intensities inhibition was observed (Fig. 2). In PAR of about 700 to 800 mmol.m^{-2}.s^{-1}, observed ETR signals were already lower than those of trees growing under the crowns. On the other hand, mean ETR of the shaded beeches planted under spruce crowns showed lower but continuously rising shape.

Discussion

Results of our study showed that differences of analyzed parameters of leaves occurred already in the first year after planting of uniformly cultivated beech planting stock planted in different positions in the young spruce forest stand. The photosynthetic apparatus of the seedlings showed a trend of acclimation to new conditions. This acclimation would lead to adjusting performance of photochemical processes in the shaded location under the spruce crown and photoprotective mechanism against excess of light energy provided within sunny patches (Robakowski and Antczak 2008).

Planting of frost sensitive target species under crowns of young spruces (optimal height of 1.5 to 2.5 meters) is recommended during reconstructions of non-native species forest stands in harsh mountain conditions (Balcar *et al.* 2007). Despite of light and water competition, positive impact on reduction of temperature extremes is expected, which was experimentally documented (Balcar and Kacálek 2008; Špulák and Souček 2010), and this can increase survival of frost-stressed plants. Because of different root architectures of spruce and beech, direct competition of roots between these species is not expected. Moreover, the European beech as a shade tolerant species should cope well with reduced light of the under-crown position.

Many plants, including the beech, tend to have larger leaves in shade (Hladká and Čaňová 2005). A significant positive trend of specific leaf mass with potential illumination found in our study corresponds with findings of Mészáros *et al.* (1998). These authors described the highest specific weight of leaves of beech, hornbeam and ash seedlings from natural regeneration on sunny clearcuts and the lowest under the forest stand. Curt *et al.* (2005) compared 4-year-old beeches growing in 4 light environments (under Scotch pine crowns and in clear cut areas). Shaded beeches had higher specific leaf area and lower specific length of roots than beeches from the sun. In our study, the average leaf area decreased not significantly from the shade to the stand gaps.

The nutrient content of leaves should follow gradual acclimatization in subsequent years. There were already found significant differences in nutrient contents among variants in the study of Špulák (2008) on differences of nutrients and chlorophyll *a* fluorescence in 12-year-old beech trees grown in identical positions in a young spruce forest stand in the Jizerské hory Mts. (under the crown, within the crown perimeter, in stand gaps). The results of the study showed significantly decreasing nitrogen content in leaves from the shade (under crown) to open gaps. Beech trees growing in the shade exhibited significantly higher concentrations of phosphorus and potassium. Calcium and magnesium concentrations tended to decrease with an increase of irradiance (Špulák 2008). The trends of the nutrient content according to the position indicated in the present study, with exception of Ca and Mg, were similar, but the differences were not significant. Absence of sig-

nificant differences can be explained by small number of mixed samples, as response to small amount of leaf biomass of plants.

In the absolute values, older plants of Jizerské hory Mts. (Špulák 2008) had less than 10 times lower content of P and 2 to 4 times more Ca in leaves compared to the results obtained in the present study. However, next year after planting, residual influence of forest nursery nutrition can be expected. Higher concentration of N in the shade and its lowering in the direction to gap conditions was found also by Johnson *et al.* (1997) and Kazda *et al.* (2004).

The maximal yield of PS II photochemistry (F_v/F_m ratio) is equivalent to the intrinsic photochemical efficiency of PSII. The mean value of F_v/F_m in non-stressed C_3 plants is considered as 0.84 (Björkman and Demming 1987). The mean of this parameter in the beeches planted under crowns of spruce trees was higher. A decreasing trend of maximal yield with an increase of potential irradiance corresponds with e.g. the results of Einhorn *et al.* (2004) on naturally regenerated beeches. Absorptivity parameter reflects leaf absorptivity of photosynthetically active light, therefore the parameter as determined by Imaging-PAM may be considered a close estimate of PAR-absorptivity (Walz 2003). The plants in our study did not show significant differences in absorptivity of photosynthetically active radiation.

Exposure of leaves to light levels exceeding a level that can be utilized for photosynthesis can result in photoinhibition (Ögren 1991; Einhorn *et al.* 2004). The leaves of beeches planted in stand gaps and into the perimeter of spruce trees showed sustained decrease of ETR at higher PAR values. However, photoinhibition is typically described in leaves grown in low-light environments, when exposed to sustained increases in light intensity (Rosenquist *et al.* 1991). Despite low statistical differences, higher build-up to photoinhibition of the beeches exposed to the sun compared to shaded ones was observed in the simulated conditions of forest nursery in our forest research station during the whole vegetation period of 2008 (unpublished data of Martincová). Higher maximal values of ETR of the beeches growing in sunlight corresponded with the results of Wyka *et al.* (2007), who described this state in selected deciduous and coniferous tree species. Robakowski and Antczak (2008) described photochemical responses of beech and fir saplings growing under larch and spruce canopies. Leaves of the sap-

lings acclimated to irradiance under open larch canopy, showed higher photosynthetic efficiency and more efficient photoprotective mechanism than those in the shade of denser spruce canopy. Both species were able to use efficiently light patches of low intensity, but after highlight stress beech leaves from the larch stand recovered more dynamically in quantum yield of PS II photochemistry when compared with those from the silver fir stand.

In our study, beech individuals planted under spruce crowns showed significantly higher non-photochemical quenching. Non-photochemical quenching parameters are all related to non-radiative dissipation of excitons as heat through various mechanisms in the antenna and reaction center (Rosenquist and van Kooten 2003). These results correspond with research on older saplings also growing under 2 different canopies (Robakowski and Antczak 2008).

Acclimatization capability of beech seedlings to changed light environment was also presented by Tognetti *et al.* (1997). These authors investigated behavior of beech trees transported from the shade to the sun and vice versa and found lack of pronounced high-light acclimation in seedlings grown in the growth chamber. This phenomenon was explained as a threshold-type relationship between acclimation capacity and a level of damage. The authors meant that survival of beech seedlings following gap formation may depend more on competition from successional species with high photosynthetic rates than on acclimation of the photosynthetic apparatus of seedlings which developed in the shade. The results of a study describing photosynthetic acclimation of beech seedlings after major windstorm in France (Reynolds and Frochot 2003) indicated that after two years of observations, acclimation of shaded leaves to full sunlight was a gradual process occurring over successive growing seasons. Our study showed that adaptation/acclimation changes to new light environment started already in the first year after replanting.

Conclusions

Fagus sylvatica planted in different positions in the young spruce stand situated in upper mountain location showed different photosynthetic performance of leaves already in the first year after planting. Depend-

ing on current light conditions, the beech transplants were able to form morphologically as well as physiologically specific leaves, regardless of insignificant differences in the nutrient content. Our results indicated that bud forming processes in late spring predispose architecture (number and position) of leaves, but these were only partially responsible for physiological performance of leaves next year after planting. Photosynthetic performance of beech trees is significantly influenced by actual growing conditions in the vegetation period, and a great part of acclimation occurs already first year after planting – change of the light conditions. The study confirmed greater efficiency of photochemical processes of seedlings planted into stand gaps, however these seedlings were more prone to photoinhibition. We speculate that this phase of gradual acclimation of the assimilation apparatus can cause physiological weakening. Considering the demand to reduce risk of late frosts in the mountains, trees should be planted in micro-sites where most of their ecological needs are fulfilled. Beeches planted into reduced light under crowns or within the crown perimeter of young spruces in stands being converted showed no serious disadvantage when photosynthetic performance assessed by chlorophyll *a* fluorescence is considered.

Acknowledgement

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